PLANT SUCCESSION IN THE BERKELEY HILLS, CALIFORNIA

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Secondary plant succession following the abandonment of crop agriculture has been widely studied. Little attention, however, has been given to the study of succession following the elimination of grazing livestock. Many parts of the California Coast Ranges that are adjacent to larger metropolitan areas have a history of heavy grazing followed by the elimination of livestock (Aschmann, 1959). The land use history of the Berkeley Hills of Alameda and Contra Costa counties, California, is typical of this pattern. Livestock were introduced into this area in 1776 (Halley, 1876) and their numbers increased to a peak of 185,503 animals in the decade from 1920 to 1930 (Burcham, 1957). The decline since 1930 has resulted in part from the removal of certain lands available for grazing following establishment of a watershed system and the East Bay Regional Parks. Significant vegetational changes followed elimination of grazing from the parks. The purpose of this study was to determine the pattern of succession following elimination of grazing on grassland areas in the Berkeley Hills.

Study Area

The Berkeley Hills are east of San Francisco Bay adjacent to the cities of Berkeley and Oakland. They are dominated by a series of long ridges oriented along axes running from northwest to southeast. Elevations range from 90 to 580 meters.

The dominant soil type throughout the area is Los Osos adobe clay (Carpenter and Cosby, 1939). It ranges in depth from a few decimeters to about two meters and has an average depth of one meter. This soil has developed from sandstones and shales and to a lesser extent from conglomerates. Owing to the soft nature of the parent material, stony slopes, rock outcrops, and loose rocks are not abundant. The soil is subject to landslides during periods of heavy rain and as a result the surfaces of many hillsides are broken and irregular.

The area has a Mediterranean climate characterized by occurrence of frequent summer fogs and especially cool summers with no month having a mean temperature greater than 18°C (Russell, 1929). During winter, weather is dominated by a cyclone system that brings rain. Occasional intrusions of dry, cool polar air masses also occur. A climatic summary for Berkeley, the nearest station with long term records available, shows an average temperature of 9.1°C for January and 16.4°C for July based on 67 years of records. During this period, extreme maximum and mini-

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mum temperatures recorded were 41.1°C and −4.1°C, respectively. Average annual precipitation is 56.8 cm with averages of 11.7 cm for January and 0.02 cm for July (U.S.D.C., 1972).

Vegetation of the Berkeley Hills as a complete physiographic unit has not been investigated. Certain portions of the area have, however, been studied (McMinn, 1916; Constance, 1932; Harris, 1927; Wright, 1928; Kraebel, 1934; Wilson and Keniston, 1942; McBride and Heady, 1968). These studies serve as a useful background in recognizing vegetation types as well as a basis for successional study. For the purpose of this report, the vegetation of the Berkeley Hills was classified into eleven types (Table 1). These were based on life form and a few dominant species. Some description, however, will be presented to complete the picture of the study area.

The grassland type occurs on a variety of exposures but is most frequently found on southwest-facing slopes. *Avena fatua, Bromus mollis,* and *Lolium multiflorum* are the dominant grasses in Berkeley Hills grasslands. Broad-leafed herbaceous species such as *Medicago polymorpha, Erodium cicutarium,* and *Geranium dissectum* are also common. All of these are exotic species that have invaded and dominated the Berkeley Hills grasslands in conjunction with the introduction of livestock from Europe (Burcham, 1957).

The baccharis brushland type varies in species composition from stands composed entirely of *Baccharis pilularis* in the shrub layer to stands in which *B. pilularis* and *Rhus diversiloba* are dominants. *Rhamnus californica* and *Rubus vitifolius* are also common in this type but seldom achieve a dominant position. The understory of baccharis brushland is characterized by an absence or very low density of herbaceous species. The type and density of herb layer species varies with the degree of crown closure and age of the baccharis brushland. Young, fairly open

Table 1. Vegetation Types in the Berkeley Hills.

Vegetation Type	Percent Area Covered	Dominant Species
Grassland	43.0	*Avena fatua, Bromus mollis, Lolium multiflorum*
Baccharis Brushland	21.0	*Baccharis pilularis, Rhus diversiloba*
Oak Woodland	17.2	*Quercus agrifolia*
Bay Woodland	7.4	*Umbellularia californica*
Redwood Forest	2.3	*Sequoia sempervirens*
Riparian Woodland	0.5	*Salix lasiolepis*
Knobcone Pine Woodland	0.5	*Pinus attenuata*
Manzanita-Chamise Brushland	0.4	*Arctostaphylos crustacea, Adenostema fasciculatum*
Coastal Sagebrush	0.1	*Artemisia californica*
Plantations:		
Eucalyptus	6.8	*Eucalyptus globulus*
Monterey Pine	0.8	*Pinus radiata*

stands exhibit an herb layer composed of grasses and broadleaf herbaceous species similar to those occurring in the Berkeley Hills grasslands. Older stands with complete crown closure are characterized by a very sparse herb layer. In many of these stands, herb density is less than one plant per ten square meters. *Rubus vitifolius, Scrophularia californica,* and *Satureja douglasii* are the most common species observed in the herb layer flora of the baccharis brushland type.

The oak woodland type is dominated by *Quercus agrifolia.* In most stands, *Q. agrifolia* is the only tree species. On moist sites *Acer macrophyllum* and *Umbellularia californica* may be associated with the dominant oak. *Arbutus menziesii* is found in the oak woodland type on drier sites. The shrub layer in the oak woodland is dominated by *Rhus diversiloba,* which often reaches a height of two meters or may grow as a vine up into the crowns of the trees. *Rhamnus californica, Rubus vitifolia, Symphoricarpos mollis, Corylus cornuta* var. *californica, Heteromeles arbutifolia, Physocarpus capitatus,* and *Rubus parviflorus* also occur as shrub layer species in the type. The herb layer of the oak woodland is rich in species in contrast to that of the baccharis brushland. The commonly occurring species are *Dryopteris arguta, Smilacina racemosa* var. *amplexicaulis, Galium aparine, Satureja douglasii,* and *Pteridium aquilinum* var. *pubescens.*

Umbellularia californica is the single tree dominant of the bay woodland type. A shrub layer does not normally develop beneath the *U. californica* canopy. Occasionally *Rhus direvsiloba* and *Symphoricarpos mollis* may be encountered but their occurrence is rare. The herb layer of the bay woodland type can be absent or represented by a number of species tolerant to conditions of low light intensity. Among these are *Disporum hookeri, Trientalis latifolia,* and *Smilacina racemosa* var. *amplexicaulis.*

The other vegetation types listed in Table 1 will not be described. They represent a small but interesting proportion of the vegetation of the Berkeley Hills. They also are not part of the pattern of secondary plant succession described in this paper.

Methods

Several methods are available for determining the pattern of plant succession. The most complete review of these methods was presented by Ludi (1930). Daubenmire (1968) discussed the more commonly used methods in his textbook on plant communities. Methods have been classified as "direct" when they are based on observation of succession on permanent plots or through the use of historical documents that give details of former vegetation. "Indirect methods" involve inference of the successional pattern. Inference is based on data or observations taken at a single time during the successional sequence. Choice of a method in any successional study depends upon availability of time, historical documents, and type of vegetation under study.

The approach used in this study was to determine the successional

position of each of the four major vegetation types in areas where grazing livestock had been eliminated. Use of "direct" methods was thought to be more positive and these methods were given priority in the study. Where sources of earlier conditions of vegetation were available, a resurvey of permanent plots or a remapping of vegetation was undertaken to identify vegetation change. When these "direct" methods could not be applied, two "indirect" methods were used. These were the stand age analysis (Clements, 1905) and maturity index (Pichi-Sermolli, 1948) methods.

Stand age analysis involves determining the age of plants in a stand and then plotting the frequency distribution of age classes for each species. Generally, climax species are characterized by J-shaped curves and sub-climax species by bell-shaped curves (Meyer and Stevenson, 1943; Braun, 1959).

Maturity index is based on the assumption that uniformity in the distribution of species in a stand increases as stands become more mature. The index is defined as the sum of the frequency percentages of all species in a stand. The index ranges from 0 to 100; the higher the index, the more mature is the stand (the closer the stand is to climax). Pichi-Sermolli (1948) has demonstrated that this relationship exists for successional sequences occurring in Europe.

Results

Grassland. In studying vegetation change in grasslands removed from grazing two direct methods were used. The first was remeasurement of permanent line transects established in 1952 by Harold F. Heady (University of California, Berkeley). These line transects are 6.35 m long and extend perpendicularly across a grassland-baccharis brushland boundary. In 1965, 23 of the original 24 transects were re-examined (one could not be located) and the position of the grassland-baccharis brushland boundaries were replotted. During a 13-year period the baccharis brushland front had moved into the grassland an average of five meters. This expansion involved both the enlargement of existing plants and the addition of new plants.

The second direct method used in the grassland type involved the examination of historical documents. A map prepared by Harris (1927) delineated large areas of grassland where baccharis brushlands now dominate. Part of the area shown on the Harris Map—that part now included in Tilden Park, an area closed to grazing since the mid 1930's—was remapped in 1963. In 1927, this area, according to the Harris map, contained approximately 50 hectares of baccharis brushland. In 1963, it contained approximately 270 hectares, an increase of 220 hectares on land formerly supporting the grassland vegetation type. This change indicates a succession from the grassland type to the baccharis brushland type where livestock grazing has been eliminated.

Grasslands currently being grazed in the Berkeley Hills are relatively

free of *Baccharis pilularis* as well as other brush species. Field observations suggest that cattle browse and often pull up *B. pilularis* seedlings that they encounter in grasslands. This grazing behavior is especially evident in summer when annual grasses have dried and *B. pilularis* seedlings are among few green plants in the grassland. This impact of livestock in preventing establishment of *B. pilularis* in grassland is further evident when one compares land currently being grazed outside of the East Bay Regional Parks with those adjacent to former grasslands inside the park boundaries. The latter grasslands have been or are rapidly being invaded by *B. pilularis*.

Baccharis Brushland. Field reconnaissance of several baccharis brushlands suggested that both *Quercus agrifolia* and *Umbellularia californica* were becoming established as seedlings under the canopy of the brush species. In some brushfields it was also possible to see tree saplings extending above the canopy of the brush.

Two early vegetation maps were used to document the change indicated by the field reconnaissance. McMinn (1916) mapped Hamilton Gulch as having an area of baccharis brushland in the upper end of the gulch. His map indicates that two *Quercus agrifolia* trees were present in the upper portion of Hamilton Gulch (fig. 1). This area was remapped in 1967. Six additional trees of *Q. agrifolia* and nine of *Umbellularia californica* were found in the baccharis brushland. The remapping also illustrates an extension of the baccharis brushland into areas dominated by grassland in 1916.

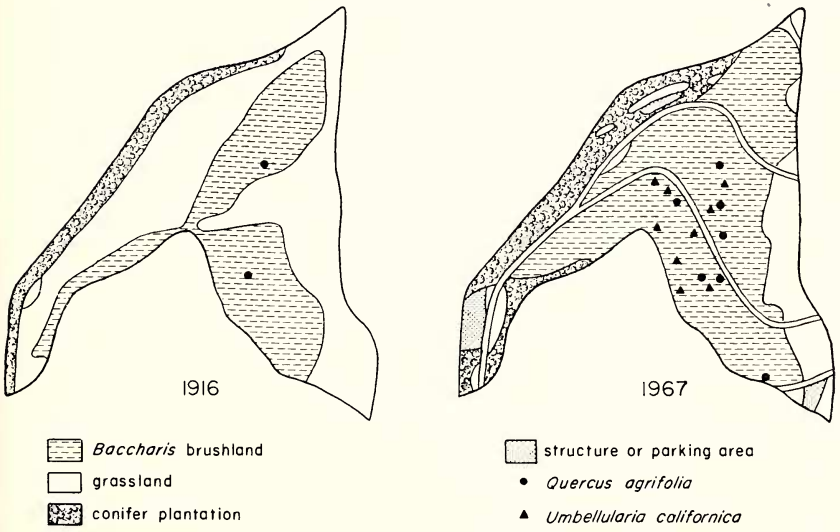

FIG. 1. Comparison of distribution of vegetation types in Upper Hamilton Gulch in 1916 and 1967.

A vegetation map of a portion of Strawberry Canyon drawn by Wright (1928) shows a large baccharis brushland in which no trees were present. This area was also remapped in 1967; nine *Quercus agrifolia* and 19 *Umbellularia californica* trees were present.

This direct use of historical documents involved baccharis brushlands that were removed from grazing in the 1920's. In areas where livestock are free to graze in baccharis brushlands, the animals seldom venture into the brushlands except along established trails. Their browsing of large plants is minimal; however, they do have an impact on seedlings along trails through the brushlands and along the margins of stands. Field reconnaissance of older baccharis brushlands accessible to livestock also indicate an invasion by *Quercus agrifolia* and *Umbellularia californica*. It would appear that the baccharis brushland type is a successional type with or without the influence of livestock. Woodland types will replace it over time. Occurrence of rather extensive older brushfields throughout the Berkeley Hills suggests that factors other than grazing have been responsible for their maintenance. All brush species common to this type are vigorous sprouters following fire (Sampson and Jesperson, 1963). Field observations of fire occurring in the Berkeley Hills over the past ten years suggest that wildfires can rejuvenate decadent baccharis brushlands. *Quercus agrifolia* and *U. californica* saplings occurring in brushfields occasionally succumb to wildfires. Those individuals that do sprout following fires are somewhat slowed down in their effort to attain tree size and form. Recurrent fire would tend to maintain a baccharis brushland. I estimate that the succession from baccharis brushland to a woodland type would be expected to take place in about 50 years in the absence of recurrent wildfires. Type of woodland (oak, bay, or mixed) depends upon those variables that affect the dispersal of tree seeds into the baccharis brushlands.

Woodland Types. No record could be found of any permanent plots having been established in the woodland types in the Berkeley Hills. Early vegetation maps of the area do not distinguish between oak woodlands and bay woodlands (McMinn, 1916; Harris, 1927; Wright, 1928; Constance, 1932; Kraebel et al., 1934; Wilson and Keniston, 1942). Therefore, indirect methods were employed to study the successional trends in the oak and bay woodlands. Specifically the stand age analysis and maturity index methods were used.

A stand age analysis was made on five oak woodland and five bay woodland stands. In each stand a 0.022 hectare circular plot was established. The age of all trees over 5 cm in diameter at breast height on each plot was determined by ring counts on increment cores taken 15 cm above the ground. All trees under 5 cm in diameter were cut off at ground level and their ages determined by ring counts on the severed sections. An age distribution curve was prepared for the oak woodlands by averaging data from the five plots (fig. 2). Likewise, a curve was prepared

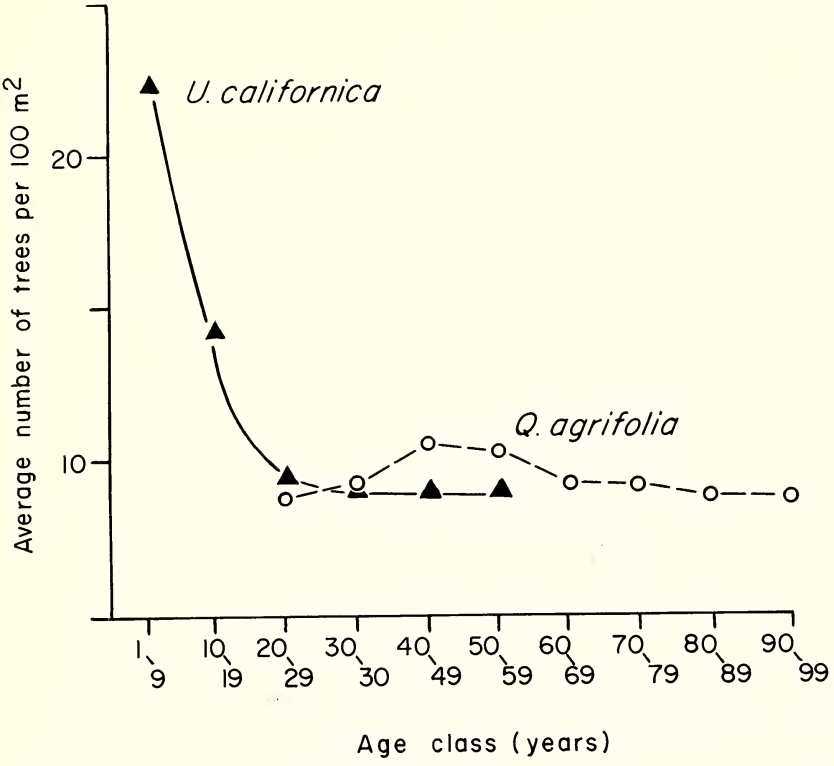

FIG. 2. Distribution of age classes of *Quercus agrifolia* and *Umbellularia californica* in five oak woodlands in the Berkeley Hills.

for the bay woodland (fig. 3). To draw the curve for each species, the average number of trees in each age class was plotted over the age class. These graphs indicate that *Quercus agrifolia* is being replaced by *Umbellularia californica* in the oak woodland type while *U. californica* is replacing itself in the bay woodland type. In both graphs *U. californica* exhibits a J-shaped curve, which is characteristic of climax species. The shape of the curve suggests that numerous seedlings are being produced. These seedlings represent a reserve from which sapling and larger sizes are being produced as openings occur in the woodland overstory. The bell-shaped curve for *Q. agrifolia* in the oak woodland stands indicates a lack of successful regeneration during the last 20 years. Curves of this shape are characteristic of sub-climax forest species that become established over a few decades then fail to produce additional seedlings. As this cohort of trees increases in age its numbers are reduced until the species eventually disappear from the site.

The second indirect method applied in investigating the successional relationship between the oak woodland and bay woodland types was the maturity index method. Five stands of oak woodland and five stands of

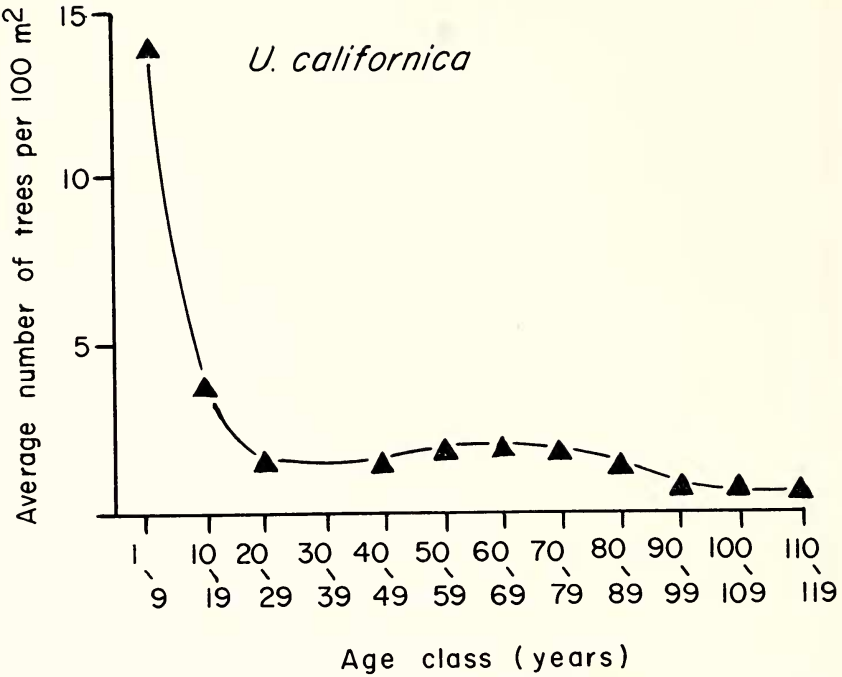

FIG. 3. Distribution of age classes of *Umbellularia californica* in five bay woodlands in the Berkeley Hills.

bay woodland occurring on northeast-facing slopes were used in determining maturity indices for each type. The frequency percentage of each species used to calculate the maturity index was based on its frequency in 100 plots (0.0929 m^2) randomly located in each stand. The average maturity index for the five oak woodlands was 7.1 and the average maturity index for five bay woodlands was 11.2 (Table 2). The higher maturity index of the bay woodland indicates a greater uniformity in the distribution of species in stands of the type. This greater uniformity suggests that the bay woodland type is more "climax like" of the two types.

Use of these indirect methods to study succession in the woodland types suggests a directional movement from oak woodland to bay woodland. Furthermore, the bay woodland type exhibits characteristics associated with climax types. The impact of cattle removal on the oak and bay woodland types is difficult to assess in the Berkeley Hills due to the high density of the deer population. Both deer and cattle exhibit a preference for *Quercus agrifolia* seedlings over seedlings of *Umbellularia californica* in the Berkeley Hills. When cattle are present they hasten succession of oak woodlands to bay woodlands due to selective pressure on *Q. agrifolia* seedlings. In the areas where livestock have been removed in the Berkeley Hills, deer hunting has generally been prohibited. The

TABLE 2. SPECIES FREQUENCIES AND MATURITY INDICES. Based on 100 plots (0.02 m^2) per stand in five stands of bay woodland and five stands of oak woodland.

Species	Frequencies									
	Bay Woodland Stands					Oak Woodland Stands				
	1	2	3	4	5	1	2	3	4	5
Disporum hookeri	67	21	26	15	18		2	2	1	1
Symphoricarpos mollis	43	11	5	14	7	5	20	27	9	8
Trientalis latifolia	40	31	21		13	16		7	9	
Umbellularia californica	28	43	18	34	17	1	3	3	4	2
Rhus diversiloba	18	16	10	17	17	30	57	14	14	31
Dryopteris arguta	18	10	20	10	11	21	2	10	19	7
Smilacina racemosa var. *amplexicaulis*	15	3	3	1		25		22	4	3
Stachys rigida	9	2	2	7	9		7			35
Rubus vitifolius	7	14	8	6	6	25	32	56	30	24
Polystichum munitum	4		26			2		1	5	2
Galium aparine	2			1	9	17	10	5	10	52
Osmorhiza chilensis	2			3	2				5	1
Satureja douglasii	1	6		8	2	2		13	1	8
Vicia gigantea	1			1				1	1	
Lathyrus vestitus		4		1		1	1	4	1	
Fragaria californica		3				1		13		
Galium californicum		1	4				2	3		4
Rhamnus californica		1				5	2	3	2	1
Holodiscus discolor		1					2			
Aster radulinus		1		4			15	17		
Tellima grandiflora			2							
Actea rubra var. *arguta*			2							1

TABLE 2,. *Continued.*

Species	Frequencies									
	Bay Woodland Stands					Oak Woodland Stands				
	1	2	3	4	5	1	2	3	4	5
Symphoricarpos rivularis			1		5				1	10
Ribes menziesii			1							
Physocarpos capitatus			1							
Saxifraga californica				2	1					
Heteromeles arbutifolia				1						
Rosa gymnocarpa				1					3	3
Sambucus caerulea				2				1	1	
Pityrogramma triangularis				1						
Pellaea mucronata				1						
Quercus agrifolia						5	6	4	3	9
Rubus parviflorus						8		4	4	5
Scrophularia californica						3		2		1
Lactuca virosa						4		1		
Chlorogalum pomeridianum						5		3		
Pteridium aquilinum var. *pubescens*						7	2	4	2	1
Prunus virginiana var. *demissa*						2				
Heracleum lanatum						1				1
Cirsium vulgare						1				1
Montia perfoliata										7
Corylus cornuta var. *californica*						1	1	2	2	
Hypochoeris glabra						1				2
Cornus stolonifera							3			
Aesculus californica							2			4

Sanicula bipinnatifida					2		1		3	17
Linaria canadensis var. *texana*							1			
Agrostis hallii							1	3		7
Artemisia douglasiana							1			
Marah fabaceus							1			
Poa pratensis								3		2
Baccharis pilularis								2	1	
Dentaria californica					19			1		10
Helenium puberulum								1		
Gutierrezia californica								1	1	
Stellaria media									2	2
Acer macrophyllum									1	
Cynoglossum grande										8
Ribes divaricatum									1	
Sonchus asper										5
Prunus emarginata									1	
Polypodium californicum										1
Vicia angustifolia									1	
Sanicula crassicaulis										2
Trillium ovatum										1
Sum of Frequencies	255	168	150	130	185	189	174	233	144	260
Number of Species	14	16	16	20	16	24	23	31	32	35
Maturity Index	18.2	10.5	9.4	6.5	11.6	7.0	7.6	7.5	4.5	7.9
Average Maturity Index			11.2					7.1		

TABLE 2. *Continued.*

Species	Frequencies									
	Bay Woodland Stands					Oak Woodland Stands				
	1	2	3	4	5	1	2	3	4	5
Symphoricarpos rivularis			1		5				1	10
Ribes menziesii			1							
Physocarpos capitatus			1							
Saxifraga californica				2	1					
Heteromeles arbutifolia				1						
Rosa gymnocarpa				1					3	3
Sambucus caerulea				2				1	1	
Pityrogramma triangularis				1						
Pellaea mucronata				1						
Quercus agrifolia						5	6	4	3	9
Rubus parviflorus						8		4	4	5
Scrophularia californica						3		2		1
Lactuca virosa						4		1		
Chlorogalum pomeridianum						5		3		
Pteridium aquilinum var. *pubescens*						7	2	4	2	1
Prunus virginiana var. *demissa*						2				
Heracleum lanatum						1				1
Cirsium vulgare						1				1
Montia perfoliata										7
Corylus cornuta var. *californica*						1	1	2	2	
Hypochoeris glabra						1				2
Cornus stolonifera							3			
Aesculus californica							2			4

Sanicula bipinnatifida					2		1		3	17
Linaria canadensis var. *texana*							1			
Agrostis hallii							1	3		7
Artemisia douglasiana							1			
Marah fabaceus							1			
Poa pratensis								3		2
Baccharis pilularis								2	1	
Dentaria californica					19			1		10
Helenium puberulum								1		
Gutierrezia californica								1	1	
Stellaria media									2	2
Acer macrophyllum									1	
Cynoglossum grande										8
Ribes divaricatum									1	
Sonchus asper										5
Prunus emarginata									1	
Polypodium californicum										1
Vicia angustifolia									1	
Sanicula crassicaulis										2
Trillium ovatum										1
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Average Maturity Index			11.2					7.1		